

Plantlet Formation in Tropical Montane Ferns: A Preliminary Investigation

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Ferns exhibit a variety of reproductive mechanisms. Sexual reproduction and gametophytic apomixis occur via spores, which are dispersed and germinate to form gametophytes. Many ferns also reproduce vegetatively, producing new ramets through rhizomatous growth, fragmentation and reestablishment, and the formation of plantlets. These ramets are genetically identical to the parent sporophyte and are morphologically complex prior to separation from the parent sporophyte. Genera known to produce viviparous plantlets on sporophyte fronds include *Adiantum*, *Asplenium*, *Camptosorus*, *Cystopteris*, *Diplazium*, *Tectaria*, & *Woodwardia* (Page 1979); plants that grow in sheltered habitats in moist forests are the most likely to produce plantlets. Page (1979) notes that vivipary is common in mid-mountain forests; in this study we compare two such forests. The objectives of our study were to survey the incidence of plantlet production in ferns of two tropical montane forests in Costa Rica, and to determine if plantlet production is more common in the higher, wetter forest than the lower, dryer one.

METHODS

We compared two sites in the vicinity of the Monteverde Cloud Forest Reserve (Puntarenas Province, Costa Rica). The Campbell's Woods site is classified as Premontane/Lower Montane Forest Transition (Holdridge, 1967) and is lower (1460 – 1500 m) and dryer than the Nuboso Trail Woods (1520 – 1560m), which are classified as Lower Montane Forest (true "Cloud Forest"). We sampled four 3x3 m plots in each forest, recording for each individual fern sporophyte encountered: species, reproductive status, number of fronds, and cover (area for terrestrial ferns, vertical height for epiphytes). Juveniles were not included.

We defined the various measures of frequency and abundance as follows: Density (D) = the number of individuals per area sampled; relative density (RD) = density of the species divided by the total D for all individuals times 100; frequency (F) = number of plots in which the species occurred divided by the total number of plots sampled; relative frequency (RF) = frequency of the species divided by the total of the F values for all species times 100; and importance (I) = the sum of RD and RF divided by 2. We calculated these for each species at each site.

Fieldwork was done in May 1988. Voucher specimens were determined at the herbarium of the Museo Nacional de Costa Rica by Mike Grayum and Suzanne Koptur, and remain in Koptur's collection in the FIU herbarium.

RESULTS

We encountered in total 32 species of ferns in 15 genera (Table 1, Table 2). Six of these species were observed to produce plantlets. Although many species of *Asplenium* are known to make plantlets, we only observed this phenomenon in *A. harpeodes* and *A.*

Table 1. Fern species in lower montane wet forest, Campbell's Woods: Relative density (RD), relative frequency (RF), importance (I), and reproduction (R).

Species	RD	RF	I	R
<i>Asplenium auritum</i> Sw.	2.63	4.55	3.59	none
<i>A. barbaense</i> Hieron	10.52	4.55	7.53	spores
<i>A. gomezianum</i> Lellinger	5.27	4.55	4.91	spores
<i>A. pteropus</i> Kaulf.	2.63	4.55	3.59	spores
<i>Blechnum ensiforme</i> (Liebm.) C.Chr.	2.63	4.55	3.59	none
<i>Campyloneurum sphenodes</i> (Kunze ex. Kl. Fee)	5.27	4.55	4.91	none
<i>Ctenitis atrogrisea</i> (C. Chr.) Ching	2.63	4.55	3.59	spores
<i>C. hemsleyana</i> (Baker) Copeland	2.63	4.55	3.59	spores
<i>C. subincisa</i> (Willd.) Ching	2.63	4.55	3.59	spores
<i>Diplazium urticifolium</i> Christ	2.63	4.55	3.59	plantlets
<i>Lomariopsis latiuscula</i> (Maxon) Holtt.	15.79	18.18	16.98	spores
<i>Polybotrya osmundacea</i> H. & B. ex Willd.	10.52	4.55	7.53	none
<i>Selaginella anceps</i> Presl.	2.63	4.55	3.59	none
<i>Thelypteris hatchii</i> A. R. Smith	2.63	4.55	3.59	spores
<i>Trichomanes radicans</i> Sw.	7.89	9.09	8.49	spores
<i>T. reptans</i> Sw.	21.04	13.64	17.34	spores

Table 2. Fern species in lower montane rain forest, Nuboso Woods: Relative density, relative frequency, importance, and reproduction.

Species	RD	RF	I	R
<i>Asplenium cirrhatum</i> L. C. Rich ex Willd.	1.06	2.22	1.64	spores
<i>A. gomezianum</i> Lellinger	1.06	2.22	1.64	spores
<i>A. harpeodes</i> Kunze	3.19	4.44	3.82	both
<i>A. maxonii</i> Lellinger	9.58	6.67	8.13	both
<i>A. pteropus</i> Kaulf.	17.02	6.67	11.85	spores
<i>Bolbitis oligarchia</i> (Baker) Hennipman	2.13	2.22	2.18	both
<i>Campyloneurum sphenodes</i> (Kunze) Fee	4.26	6.67	5.47	spores
<i>Ctenitis atrogrisea</i> (C. Chr.) Ching	1.06	2.22	1.64	spores
<i>C. hemsleyana</i> (Baker) Copeland	4.26	6.67	5.47	spores
<i>Cyathea fulva</i> (Mart. & Gal.) Fee	1.06	2.22	1.64	none
<i>Diplazium cristatum</i> (Desr.) Alston	1.06	2.22	1.64	spores
<i>D. lehmanii</i> Hieron	1.06	2.22	1.64	plantlets
<i>D. multigemmatum</i> Lellinger	3.19	2.22	2.71	both
<i>D. urticifolium</i> Christ	17.02	6.67	11.85	plantlets
<i>D. werckleanum</i> Christ	2.13	4.44	3.29	none
<i>Elaphoglossum eximium</i> (Mett.) Christ	1.06	2.22	1.64	spores
<i>E. latifolium</i> (Sw.) J. Sm.	1.06	2.22	1.64	spores
<i>Grammitis taxifolia</i> (L.) Proctor	1.06	2.22	1.64	spores
<i>Hymenophyllum consanguineum</i> Morton	1.06	2.22	1.64	spores
<i>Lomariopsis latiuscula</i> (Maxon) Holtt.	7.45	8.89	8.17	spores
<i>Pecluma pectinata</i> (L.) Proctor	1.06	2.22	1.64	spores
<i>Peltapteris peltata</i> (Swartz) Morton	3.19	4.44	3.82	spores
<i>Polypodium fraxinifolium</i> Jacq.	1.06	2.22	1.64	none
<i>Thelypteris hatchii</i> A. R. Smith	3.19	4.44	3.82	spores
<i>Trichomanes reptans</i> Sw.	10.64	8.89	9.77	spores



Fig. 1. Plantlet production from leaf tips in *Asplenium maxonii*. The plantlet is not shaded in the drawing. The bar scale is 2 cm.

maxonii; in both species, elongated leaf-tips produced plantlets (Fig. 1). Three of the four *Diplazium* species we encountered were observed with plantlets (*D. lehmanii*, *D. multigemmum*, and *D. urticifolium*); all of these develop buds on the abaxial surface of the frond at the intersection of a major vein and the midrib, the plantlet developing first roots, then leaves that curve around to the adaxial leaf surface (Fig. 2). The unusual *Bolbitis oligarchia* has dimorphic fronds and trifoliate leaves, and plantlets are formed in the middle of the 3 leaflets on the adaxial surface of the trophophylls (leaves not specialized for spore production) (Fig. 3). We also observed plantlets on *Lomariopsis latiuscula*, but not on any individuals in our study plots.

We found 16 species in 10 genera of ferns in plots sampled in the lower elevation wet forest site, Campbells Woods (Table 1). Ten species were found sporing, and only one species, *Diplazium urticifolium*, had plantlets at the time of our census. The species with the greater importance values reproduced by spores alone.

Table 3 – Comparative importance of fern species occurring at both sites. I = importance, C = Campbell's Woods, N = Nuboso Woods.

	I (C)	I (N)	Reproduction
<i>Asplenium gomezianum</i>	4.91	1.64	spores
<i>A. pteropus</i>	3.59	11.85	spores
<i>Campyloneurum sphenodes</i>	4.91	5.47	spores
<i>Ctenitis atrogrisea</i>	3.59	1.64	spores
<i>C. hemsleyana</i>	3.59	5.47	spores
<i>Diplazium urticifolium</i>	3.59	11.85	plantlets
<i>Lomariopsis latiuscula</i>	16.98	8.17	spores
<i>Thelypteris hatchii</i>	3.59	3.82	spores
<i>Trichomanes reptans</i>	17.34	9.77	spores

Of 25 species in 15 genera found in the higher elevation rain forest site (Nuboso), 20 species were making spores, and 6 species were making plantlets (Table 2). Four species had both spores and plantlets, 2 species had plantlets only. Of the species with the greater importance values, two (*Asplenium maxonii* and *Diplazium urticifolium*) produced plantlets; other plantlet producers had relatively low importance values.

Nine species occurred in plots at both sites (Table 3). Only one species of fern was found bearing plantlets in both forests (*Diplazium urticifolium*).

The properties of the fern species at the two sites are compared in Table 4. There were more species at the higher elevation site, and a larger proportion of species producing plantlets (24% vs. 6%). A larger proportion of ferns from the Nuboso site were sporulating (80% vs. 63%), and 16% had both plantlets and spores. A larger proportion of ferns in Campbells Woods were non-reproductive (31% vs. 12%).

Similar comparisons done on an individual plant basis are less dramatic (Table 5). For plantlet production on individuals, Fisher's exact test (2-tailed) is significant ($p = .024$); 18% of individuals in Nuboso Woods produce plantlets, versus only 3% in Campbells Woods. Spore production does not differ significantly between sites; 32% of individuals in Nubosos Woods versus 45% in Campbells Woods.



Fig. 2. Plantlet production on fronds in *Diplazium urticifolium*. From left to right: tiny developing frond of plantlet on abaxial surface of parent sporophyte frond; plantlet grows, with 4 fronds; two plantlets on old frond ravaged by time and herbivores; plantlet rooted in soil. The plantlets are not shaded in the drawing. The bar scale is 2 cm.

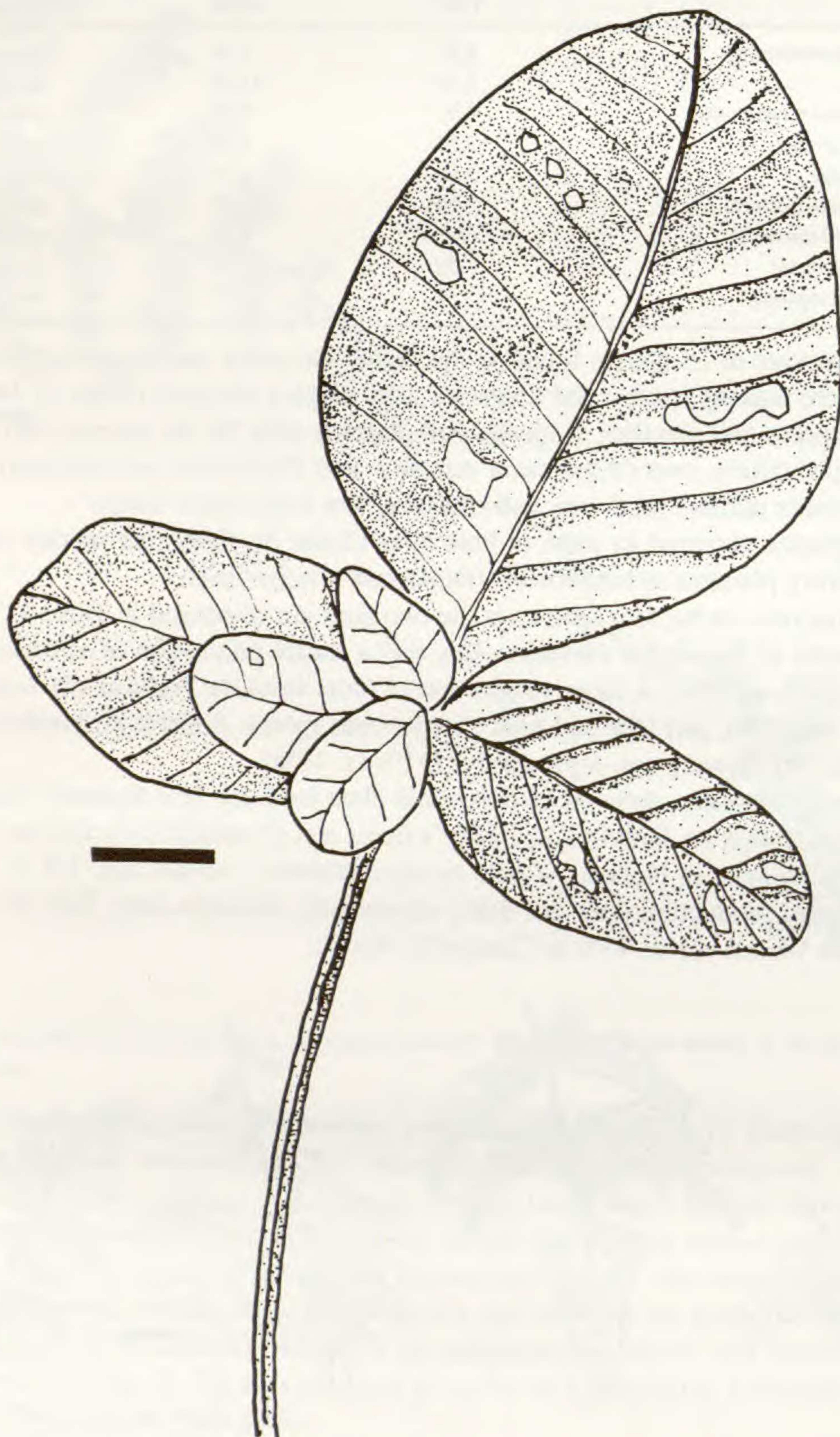


Fig. 3. Plantlet production in center of frond of *Bolbitis oligarchia*. The plantlet is not shaded in the drawing. The bar scale is 2 cm.

Table 4 – Reproductive status of fern species encountered in plots (4 replicates in each forest type).

	\bar{x} + s.d.		Total (Proportion)	
	Nuboso	Campbells	Nuboso	Campbells
Total species	11.5 + 2.9	5.5 + 1.3	25 (1.0)	16 (1.0)
Epiphytic with spores	6.5 + 1.3	2.8 + 9.6	20 (.80)	10 (.63)
with plantlets	2.3 + 1.7	.3 + .5	6 (.24)	1 (.06)
with both	1.0 + 1.1	0	4 (.16)	0 (0)
Non-reproductive	9.0 + 7.5	3.3 + 1.0	3 (.12)	5 (.31)

Table 5 – Reproductive status of individual fern plants encountered in plots (4 replicates in each forest type).

	\bar{x} + s.d.		Total (Proportion)	
	Nuboso	Campbells	Nuboso	Campbells
Total individuals	26.2 + 6.7	10.5 + 1.3	94 (1.0)	38 (1.0)
with spores	7.5 + 1.3	4.3 + 2.6	30 (.32)	17 (.45)
with plantlets	4.2 + 4.0	0.3 + 0.5	17 (.18)	1 (.03)
with both	1.0 + 1.1	0	4 (.04)	0 (0)
Non-reproductive	14.2 + 10.4	5.5 + 2.9	57 (.60)	22 (.58)

DISCUSSION

Our study revealed plantlet production to be more common in a wetter, higher elevation tropical montane forest than in a lower, dryer montane forest. It has been reported that plantlet production under cultivation conditions increases with very high humidity (Farrar, 1968; Mickel, 1976). One could therefore expect that for a fern species occurring over a range of humidity, one might observe more plantlet production in the wetter parts of the range. In East Africa, plantlet production occurs in at least 30% of species (terrestrial & epiphytic) but is associated with the epiphytic habit (Faden, 1973). There was a substantial proportion of epiphytic species in both of the forests we studied, but only in the higher, wetter site did any of the epiphytic species produce plantlets at the time we sampled.

The production of plantlets may be selectively advantageous in areas where there is a continual (not necessarily high) level of disturbance, allowing the offspring to rapidly colonize exposed ground (the terrestrial species); tropical montane areas have landslides and treefalls that provide regular but unpredictable disturbance. A large sporophyte (plantlet) may be able to compete more successfully with other potential colonists than a tiny gametophyte, and would not have immediate need for free water for fertilization.

Plantlet production allows for continuation of the genotype, even if the sporophyte is ravaged by time and enemies. It is not unusual to see nearly moribund fronds of *Diplazium urticifolium*, having lost much of their leaf area to herbivores, attached to big, healthy plantlets rooted in the soil (Fig. 2). In a wet habitat, herbivore damage to a leaf may be additionally hazardous by allowing access to phytopathogens; while the disease may spread within the sporophyte plant, the plantlet may escape contamination and survive to perennate the individual.

The vegetative propagule (plantlet) must regenerate both roots and shoots, though in different ferns the propagule is derived from different organs: in *Nephrolepis*, from the stem; in *Platycerium*, from the root (Richards, et al., 1983); and in *Diplazium* (personal

observation) and *Asplenium* (Mickel, 1976), from the leaves. The production of propagules on stolons permits dispersion of the propagule some distance from the parent sporophyte (Richards, et al., 1983); plantlets produced at or near the tips of long fronds can experience similar distancing.

Our next step is to examine the incidence of plantlet production in certain species of ferns throughout their range, and to monitor the phenology of asexual and sexual reproduction throughout the year. The number of plantlets produced and their fate should also be compared among species and habitats. This will give insight into the edaphic and climatic factors that influence the reproductive strategy. Many of the genera and some of the same species encountered in our mid-elevation study also occur in lowland wet forest at Finca La Selva (Grayum & Churchill, 1987) and will provide an essential and interesting comparison.

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